Growth, Development, and Nutritional Physiology of Grasshoppers from Subarctic and Temperate Regions

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ABSTRACT

Despite the importance of developmental rate, growth rate, and size at maturity in the life history of poikliotherms, the trade-offs among these traits and selection pressures involved in the evolution of these traits are not well understood. This study compared these traits in a grasshopper, *Melanoplus sanguinipes* F. (Orthoptera: Acrididae), from two contrasting geographical regions, subarctic Alaska and temperate Idaho. The growing season in the interior of Alaska is about 80 d shorter than at low-elevation sites in Idaho. We hypothesized that the Alaskan grasshoppers would show more rapid growth and development than grasshoppers from Idaho, at the cost of greater sensitivity to food quality. On a diet of lettuce and wheat bran, grasshoppers from Alaska developed from egg hatch to adult more rapidly than those from Idaho at each of three different temperature regimes. Averaged over all temperature treatments, the weight of the Alaskan grasshoppers was about 5% less than that of the Idaho grasshoppers at the adult molt. Feeding and digestive efficiencies were determined for the final two instars using two meridic diets: one with a high concentration of nutrients and the other with the same formulation but diluted with cellulose. Alaskan grasshoppers again developed more rapidly, weighed less, and had faster growth rates than those from Idaho. Alaskan grasshoppers supported their more rapid growth by increasing postingestive efficiencies; that is, they had higher conversion rates of digested matter to biomass on the high-quality diet, greater assimilation of food on the low-quality diet, and greater efficiency of nitrogen assimilation or retention on both diets. There was no evidence that performance of Alaskan grasshoppers suffered any more than that of the Idaho grasshoppers on the low-quality diet.

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Introduction

Life-history traits of insects may be expected to vary with latitude and altitude as populations adapt to local environments. Three interrelated traits that are of fundamental importance to an organism's fitness and that often vary with length of growing season are developmental rate, growth rate, and adult size (Dingle et al. 1990; Ayres and Scriber 1994; Nylin and Gotthard 1998; Telser and Hassall 1999; Bentz et al. 2001; Fischer and Fiedler 2002; Berner et al. 2004; Gotthard 2004). Many different selection pressures may influence the evolution of these traits, including season length, juvenile and adult mortality rates, and food quality and quantity (Abrams et al. 1996; Chippindale et al. 1996; Fielding 2004*b*; Stoks et al. 2005). Rapid development potentially increases fitness by reducing generation time and by reducing the risk of mortality before reproducing. Rapid development may be achieved by some combination of maturation at a smaller size (less growth) or more rapid weight gain (faster growth). Smaller individuals are generally assumed to be less fit. Size is often positively correlated with fecundity (Roff 1992; Nylin and Gotthard 1998) and competitive ability (Belovsky and Slade 1995) in insects, although in some cases, smaller individuals may be less susceptible to predation (Belovsky et al. 1990; Branson 2005). The trade-off between size and development time can be circumvented by increasing growth rate. The generally assumed advantages of large size and rapid development lead to the expectation that growth rates in most organisms should be maximized (Arendt 1997); however, empirical evidence suggests that growth rate is seldom at its potential maximum (Margraf et al. 2003; Tammaru et al. 2004). Possible costs associated with rapid growth in insects include diminished resistance to starvation or other stresses, greater sensitivity to food quality (Stockhoff 1991; Gotthard et al. 1994), and increased predation risk (Gotthard 2000; Danner and Joern 2003; McPeek 2004; Stoks et al. 2005).

The nutritional basis for rapid growth has not received a great deal of attention (Watler 1982; Ayres and Scriber 1994; Kause et al. 1999). Faster growth may be supported by increased feeding rate, increased assimilation of food, increased efficiency in conversion of assimilated food to biomass, or some combination of the three. Because of the multiple effects of size,

developmental time, and growth rate on an organism's fitness, a better understanding of these traits and their underlying nutritional basis may provide insights into a species' ecological interactions and population dynamics (Danner and Joern 2003; Branson 2004; McPeek 2004; Stoks et al. 2005).

The grasshopper *Melanoplus sanguinipes* F. (Orthoptera: Acrididae) has an extremely broad geographical distribution, from northern Florida and Mexico to the interior of Alaska (Richman et al. 1993; Capinera et al. 2002; Pfadt 2002), making it a good candidate for comparative life-history studies. This study examines the developmental and nutritional physiology of *M. sanguinipes* from two populations: one from interior Alaska and the other from the Palouse region of Idaho. This species can overwinter only in the egg stage. Grasshoppers in Alaska reproduce in late summer, and little embryological development occurs before the onset of winter. The following summer, development resumes until the embryo enters an obligatory diapause at a late stage of development (Salt 1949; D. Fielding, unpublished data). After overwintering a second time, the eggs are then ready to hatch. Embryological diapause in *M. sanguinipes* from Idaho, in contrast, is facultative, in that diapause is averted by cool temperatures in overwintering, prediapause embryos (Fielding 2006). Thus, all viable eggs of the Idaho population hatch the following summer. Because the eggs are in various stages of development in Idaho in the spring, hatching takes place over a longer time span than in Alaska, where all eggs are at the same late stage of development in the spring of their second year.

Developmental rates of *M. sanguinipes* from Alaska are faster than was reported for this species previously (Fielding 2004*a*). It would be surprising if developmental rates in this species did not differ geographically, given that such variation has been reported for many insects, including this species (Dingle et al. 1990). The frost-free season in the interior of Alaska is about 80 d shorter than that at low-elevation sites in Idaho, 106 versus 187 d, respectively (WRCC 2004; Fig. 1). Because of the different environments, we hypothesized that grasshoppers from Alaska would develop more rapidly than those from Idaho but also that a greater sensitivity to diet quality would be associated with more rapid development. The first objective of this study was to quantify and compare developmental rate, growth rate, and size of *M. sanguinipes* from the two regions. A second objective was to determine whether more rapidly growing grasshoppers were less tolerant to nutrient stress. Another objective was to determine whether differences exist between the two populations in the nutritional physiology that may underlie any differences in growth rate, that is, food consumption, assimilation, and conversion of digested food to biomass.

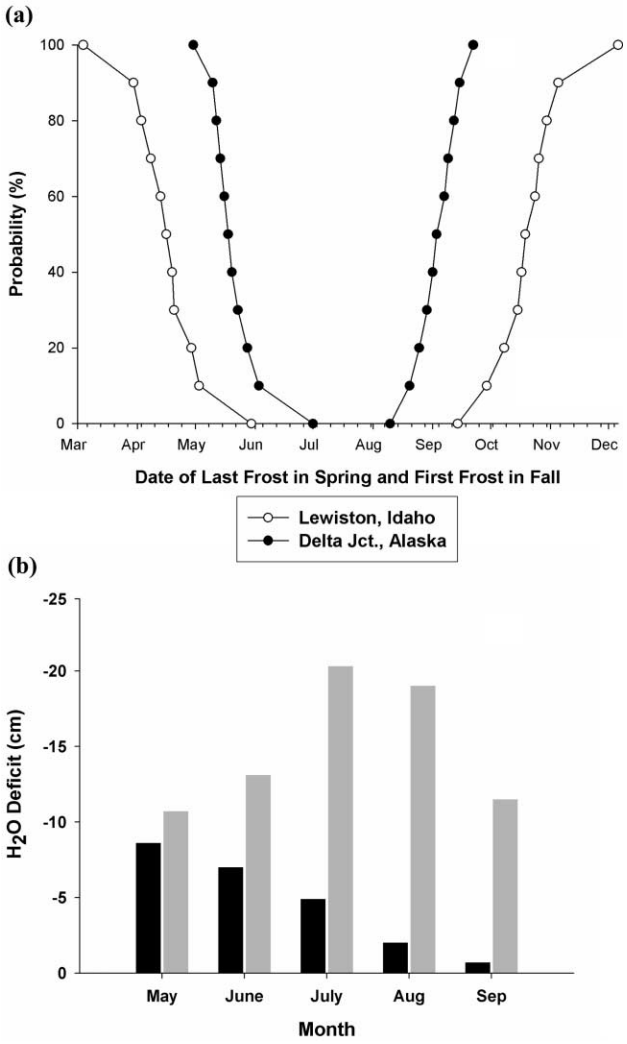

Figure 1. Mean values of climate indicators for the growing season at Lewiston, Idaho, and Big Delta, Alaska. *a*, Probabilities of the last freezing temperature in spring occurring on or after a given date and of first freezing temperature in the fall occurring on or before a given date at Lewiston (*open circles*) and Delta Junction (*filled circles*). *b*, Precipitation deficit, calculated as monthly mean precipitation total minus monthly mean of pan evaporation, at Lewiston (*gray bars*) and Delta Junction (*black bars*).

Material and Methods

Laboratory colonies were initiated with at least 200 individuals collected near Lewiston, Idaho, and Delta Junction, Alaska, as fourth and fifth instars in mid-July of 2003 and 2004. Grasshoppers were collected about 5 km southwest of the weather station of the National Oceanic and Atmospheric Administration, U.S. Department of Commerce, at Lewiston, Idaho (46.38°N, 117.02°W; 450 m elevation), and about 20 km southeast of the weather station at Delta Junction, Alaska (64.00°N, 145.73°W; 400 m elevation; WRCC 2004). All experiments were conducted on F_1- and F_2-generation offspring. Populations were reared separately to avoid outcrossing, and we assumed that no artificial selection in the laboratory environment had occurred within the one or two generations.

Growth and Development on Lettuce/Bran Diet

Developmental times from egg hatch to adult eclosion were determined for both populations at three separate temperature treatments: constant 22°C, constant 30°C, and diurnally alternating temperatures of 33° and 15°C on a 12 : 12 cycle. The 22°C treatment was selected to compare performance of the two populations near the low temperature threshold for growth and development (Parker 1930; Fielding 2004*a*). Within 24 h of hatching, grasshoppers were transferred to acetate tubes (10 cm diameter × 50 cm length) capped on both ends with wire screens, and the tubes were placed in controlled-temperature chambers. Trials at each temperature consisted of three tubes of 20 individuals each. Grasshoppers were fed ad lib. with organically grown romaine lettuce and wheat bran treated with a 6% solution of sulfamethazine sodium, as a prophylactic treatment against *Malamoeba* infections (Henry 1985), at a rate of 250 mL/kg bran. Grasshoppers were examined daily, and the numbers in each instar were recorded. Newly molted adults were removed from the tubes and weighed. Photoperiod in all trials was 16L : 8D. Light was provided by cool-white fluorescent tubes. Relative humidity in the chamber varied from 40% to 60%. Exponential growth rate was calculated as $[\log_e(\text{adult fresh weight}) - \log_e(5)]/\text{age at adult molt}$. Although hatchling weight of each individual was not measured, preliminary studies indicated that fresh weight of hatchlings of both populations was very close to 5 mg.

Nutritional Physiology on Meridic Diets

A separate experiment was conducted to obtain quantitative estimates of food consumption and utilization during the final two instars. The basic recipe for the meridic diet (a combination of natural and chemically defined ingredients) was adapted from Henry (1985). Ingredients and proportions are listed in Table 1. This base diet was diluted with cellulose to produce two foods with differing concentrations of nutrients. The N content of the diets was confirmed by dry combustion in a LECO 2000 CHNS analyzer. The base diet and the diluted diet had 4.8% and 1.6% N and 21.7% and 7.5% total nonstructural carbohydrates, respectively. This formulation resulted in a diet with a protein : CHO ratio of 1.4 : 1, which is within the range known to support rapid development and high survival in some species of Acrididae (Simpson and Raubenheimer 1993). Preliminary studies indicated that grasshoppers on the diet with the higher concentration of nutrients had weight gain and development times similar to those of grasshoppers on lettuce and bran diet. The concentration of nutrients on the low-quality diet was such that grasshoppers maintained on the diet for the final two instars survived to adult molt but showed signs of nutrient stress, such as longer developmental times and reduced weight gain. The food was dry. Water was freely available to the grasshoppers at all times. The grasshoppers were raised on lettuce and bran in groups of 10 through the early instars, as described above, at the alternating thermoperiod of 33°C for 12 h and 15°C for 12 h. This temperature regime was selected because survival and adult weights were near maximum values with this regime (Fielding 2004*a*), it simulated a natural diurnal cycle, and, by examining the grasshoppers after the daily warm phase, it provided greater resolution in observation of developmental times, assuming that no molting occurred during the 15°C phase. Within 24 h of molting to fourth instar, grasshoppers were weighed and placed into plastic food storage boxes of about 500 mL capacity, one individual per box. A quantity of dry food was weighed and placed in small trays within each box. The food was replenished as needed. Because errors are likely to be greater when smaller proportions of food are consumed (Schmidt and Reese 1986), care was taken to ensure that food was always available for the grasshoppers, but only enough so that only a small proportion of the food remained after the grasshopper molted to the adult stage. Grasshoppers were checked daily at the end of the high-temperature phase of the diurnal thermoperiod, and any adults that had molted that day were removed and weighed. Adult grasshoppers were killed by freezing and were placed in a drying oven, along with the remaining food and frass, at 60°C for 48 h or until they stopped losing weight. Dry weights to the nearest 0.1 mg of the adults, food, and frass were taken. Dry weight of the fourth instars was estimated from the dry : fresh weight ratio of a representative sample of fourth-instar grasshoppers from both populations. Nitrogen content of the grasshoppers, frass, and food was obtained with a LECO 2000 CHNS analyzer. To obtain an adequate mass (>100 mg) for N analysis of the adult carcasses, pairs of grasshoppers of the same sex and population were combined. Assimilation was calculated as weight of food consumed minus weight of feces. Net retention of N was sim-

Table 1: Ingredients and proportions of base diet

Ingredient	Proportion (g/100 g)
Casein	18.0
Wheat germ	18.5
Dried romaine lettuce	10.0
Dried ryegrass	10.0
Yeast extract	6.0
Sucrose	24.0
Corn oil	5.0
L-cystine	.5
Glycine	.7
Choline chloride	.5
Cholesterol	1.5
Ascorbic acid	2.5
Wesson salts	4.0

ilarly calculated. Analysis of weights of fourth instars, fifth instars, and adults indicated that an exponential function modeled growth rates somewhat better than a linear function. Therefore, exponential growth rates were calculated as $\log_e$ (adult weight) − $\log_e$ (fourth instar weight) divided by duration of the final two instars.

Statistical Analyses

To compare variability of different traits, coefficients of variation (CV) were calculated (SD/mean) for various traits. Differences in magnitude of CV between populations and traits were evaluated using the method of Miller (1991), as described by Zar (1999). The test statistic Z is distributed as t with infinite degrees of freedom. No variables except N percentage in frass departed significantly from normality (skewness and kurtosis < 1.0, PROC UNIVARIATE; SAS Institute 2001), and thus no data transformations were applied to these variables. The arcsine transformation was applied to N percentage in frass. A two-way ANOVA (PROC GLM; SAS Institute 2001) with population origin and sex as main effects was used to test for differences in age, development time, weight, growth rate, N percentage in frass and in grasshopper biomass, total food consumed, and food assimilated. Because interactions of diet (high and low quality) with other variables and covariables were common, separate analyses were conducted by diet rather than including diet as a main effect in ANOVAs.

ANCOVA was employed to avoid the problems associated with the use of ratios, such as food consumption per day, in the analysis of nutritional efficiencies (Packard and Boardman 1988; Raubenheimer and Simpson 1992; Raubenheimer 1995). First, ANCOVAs (PROC GLM; SAS Institute 2001) that included interaction terms between covariables and main effects were conducted. If the interaction terms between covariable and main effects were not significant ($P > 0.05$), ANCOVAs that included the covariable and main effects were conducted, and least squares means were compared. If a significant interaction occurred between covariable and main effects and plots of the data showed that regression lines for the separate populations crossed at some point within the range of covariable values, valid comparisons of the population effects could not be made by ANCOVA. If treatment effects could not be reliably evaluated by ANCOVA, the use of ratios was considered. Probability of the intercept of the regression differing from zero was assessed with a t-test (PROC GLM; SAS Institute 2001). If the intercept of the regressions was not significantly different from zero ($P > 0.05$), then ratios were employed to examine population differences. Otherwise, valid comparisons could not be made.

The following analyses were made: total food consumption during fourth and fifth instars was corrected with initial weight of the fourth instar as a covariable; rate of food consumption was analyzed by including duration of fourth and fifth instars as a covariable, along with initial weight of the fourth instar; assimilation of food, and of N only, was analyzed with consumption as the covariable; and weight gain during the fourth and fifth instars was analyzed with amount of food assimilated, or amount of N retained, as a covariable.

Results

The long-term climate data show that the growing season at Lewiston, Idaho, is typically about 80 d longer than that at Delta Junction, Alaska (Fig. 1*a*), and the summer months are drier (Fig. 1*b*) in Idaho than in Alaska. Although mean annual precipitation was similar between the two locations (32.1 and 29.4 cm, for Lewiston, Idaho, and Big Delta, Alaska, respectively), seasonal distribution of precipitation differed greatly. Mean annual temperature was 11.3° and −2.2°C for Lewiston, Idaho, and Big Delta, Alaska, respectively.

Growth and Development on Lettuce/Bran Diets

On the lettuce/bran diets, Alaskan grasshoppers completed development faster than the Idaho grasshoppers at all temperatures (Table 2). There was a significant interaction effect between population and temperature regime ($F_{2,273} = 68.3$, $P < 0.001$). Under the 30°C treatment, mean developmental time for the Alaskan population was only 3.6 d (or 14%) less than that for the Idaho grasshoppers, whereas the greatest relative difference (12.8 d, or 31%) between the populations was under the alternating 33°/15°C temperature treatment (Table 2). The rapid development of the Alaskan grasshoppers was the combined result of increased growth rate and somewhat smaller final size. The fresh weight of Alaskan grasshoppers, averaged over all temperature treatments, tended to be less than that of the grasshoppers from Idaho (mean ± SE of 297 ± 6.2 vs. 313 ± 4.2 mg; $F_{1,273} = 4.2$, $P < 0.05$). There were no significant interactions among the main effects (temperature, population, sex) on adult weight ($F_{2,273} < 1.8$, $P > 0.05$). Averaged over all temperatures, the growth rates of the Alaskan grasshoppers were greater, but there was a significant population × temperature interaction ($F_{2,273} = 22.3$, $P < 0.001$). When separate comparisons were made for each temperature regime, the largest difference in growth rates between the two populations was at the 33°/15°C alternating temperatures, and the smallest relative difference was at the 30°C constant temperature (Table 2).

Patterns of variance in developmental times and size differed between the populations. In the Alaskan population, adult weights tended to be more variable than developmental time. The CV for developmental time was less than that for weight for the Alaskan grasshoppers at each temperature ($Z > 3.3$, $P < 0.001$ in each case; Table 2). In the Idaho population, only under the alternating temperature regime was developmental time less variable than adult weight ($Z = 2.36$, $P < 0.02$; Table 2). The Alaskan developmental times were less variable than those of the Idaho population at all temperature regimes

Table 2: Developmental time (from egg hatch to adult molt), fresh weight within 24 h of adult molt, and exponential growth rate of *Melanoplus sanguinipes* from two different populations reared at three different temperatures

	Alaska			Idaho		
	Mean	SE	CV	Mean	SE	CV
22°C:						
Developmental time (d)***	49.6	90.7	4.6	70.3	1.6	14.2
Weight (mg)[a]	237.2	7.7	10.3	243.8	8.8	17.0
Growth rate ($\log_e$ (mg) d^{-1})**	.078	.004	6.4	.057	.003	22.1
30°C:						
Developmental time (d)***	22.3	.2	4.7	25.9	.7	17.3
Weight (mg)[a]	336.5	8.2	16.9	357.1	8.7	16.3
Growth rate ($\log_e$ (mg) d^{-1})***	.189	.002	6.0	.170	.003	19.4
33°/15°C:						
Developmental time (d)***	28.6	.3	7.5	41.4	.6	11.0
Weight (mg)[a]	320.8	9.0	21.0	333.5	6.9	15.5
Growth rate ($\log_e$ (mg) d^{-1})***	.149	.002	10.3	.103	.001	13.8

Note: CV = coefficient of variation.

[a] No significant difference between populations.

** Populations differ at $P < 0.01$.

*** Populations differ at $P < 0.001$.

($Z > 2.6$, $P < 0.01$; Table 2), and Alaskan growth rates were less variable than those of the Idaho grasshoppers at 22° and 30°C rearing temperatures ($Z > 3.5$, $P < 0.001$).

There was no difference in developmental time or growth rate between sexes ($F_{1,273} < 2.6$, $P > 0.05$; Table 2), but females were heavier than males (324 ± 4.9 vs. 286 ± 5.7 mg fresh weight; $F_{1,273} = 25.8$, $P < 0.001$), averaged over all temperatures. Rearing temperature had a strong effect on adult weight ($F_{2,273} = 893.6$, $P < 0.001$), with the lowest temperature treatment producing the smallest adults (Table 2). At 22°C, survival of Idaho grasshoppers (68%) was greater than that of Alaskan grasshoppers (20%). It is possible that the poor survival of Alaskan grasshoppers at 22°C was due to an undetected infection, although the colonies were regularly screened for diseases. Grasshoppers are known to be more susceptible to pathogens at cooler temperatures (Inglis et al. 1996; Elliot et al. 2002). Survival was greater than 90% at all other temperatures for both populations.

Nutritional Physiology on Meridic Diets

Grasshoppers partially compensated for the low concentration of nutrients in the low-quality diet by increasing consumption (mean consumption ± SE of the high- and low-quality diets = 339 ± 10.9 vs. 730 ± 22.4 mg food per grasshopper, averaged over population and sex; $F_{1,88} = 254.3$, $P < 0.001$). The total amount of food assimilated (consumption − feces) was greater on the low-quality diet than on the high-quality diet (176 ± 5.8 vs. 219 ± 5.4 mg per grasshopper; $F_{1,88} = 31.2$, $P < 0.001$), but the net amount of N retained was less (9.7 ± 0.3 vs. 6.7 ± 0.2 mg per grasshopper; $F_{1,88} = 71.2$, $P < 0.001$). Grasshoppers on the low-quality diet required about 1.6 d more, on average, to complete the final two instars (18.2 ± 0.43 vs. 19.8 ± 0.41 d; $F_{1,88} = 7.9$, $P < 0.01$). Averaged over population and sex, weights of grasshoppers on the higher-quality diet were greater than those of grasshoppers on the low-quality diet (83.9 ± 2.2 vs. 69.6 ± 1.8 mg dry weight of adults; $F_{1,88} = 26.2$, $P < 0.001$). Alaskan grasshoppers had a greater water content as percentage of body weight (74.8%) than the Idaho grasshoppers (71.2%; $F_{1,88} = 39.0$, $P < 0.001$). There was a significant effect of diet on water percentage in the newly molted adults, with grasshoppers on the high-quality diet having lower water percentage (71.5% vs. 74.4%; $F_{1,88} = 27.7$, $P < 0.001$). Interaction of population with diet was nonsignificant with respect to body water percentage ($F_{1,88} = 2.6$, $P > 0.10$).

Population comparisons. There were significant differences between populations for every variable measured over the final two instars, except N percentage in cadavers and feces on the low-quality diet ($F_{1,40} < 0.4$, $P > 0.05$). Alaskan grasshoppers weighed less than the Idaho grasshoppers at the beginning of the fourth instar (17.4 ± 0.8 vs. 21.0 ± 0.7 mg dry weight; $F_{1,88} = 48.1$, $P < 0.001$). The Idaho grasshoppers gained more weight than did the Alaskan grasshoppers during the fourth and fifth instars on the high-quality diet (68.3 ± 2.4 vs. 59.0 ± 2.9 mg dry weight; $F_{1,42} = 7.3$, $P < 0.01$) but not on the low-quality diet (49.9 ± 1.8 vs. 48.6 ± 2.8 mg dry weight; $F_{1,40} = 0.1$, $P > 0.10$). Duration of the fourth through fifth instar was shorter for the Alaskan grasshoppers than for the Idaho grasshoppers, on both diets (high-quality diet: 15.8 ± 0.3 vs.

20.5 ± 0.4 d; $F_{1,42} > 167.7$, $P < 0.001$; low-quality diet: 17.7 ± 0.4 vs. 21.5 ± 0.4 d; $F_{1,40} > 40.5$, $P < 0.001$). The faster developmental times during the final two instars by the Alaskan grasshoppers were enough to offset their smaller size to yield growth rates that were higher than those of the Idaho grasshoppers (high-quality diet: 0.094 ± 0.003 vs. 0.069 ± 0.002 $\log_e$ (mg) d^{-1}; $F_{1,42} = 55.5$, $P < 0.001$). Calculations with data for the low-quality diet produced similar results: faster growth rates for the Alaskan population (0.075 ± 0.003 vs. 0.055 ± 0.002 $\log_e$ (mg) d^{-1}; $F_{1,40} = 34.3$, $P < 0.001$)

As with the lettuce and bran diets, variability of developmental times from egg hatch to adult molt in the Alaskan population was less than that for adult weights on both diets (high-quality diet: CV = 5.4 vs. 17.8; $Z = 4.8$, $P < 0.001$; low-quality diet: CV = 6.5 vs. 20.7; $Z = 4.5$, $P < 0.001$). In the Idaho population, variability of developmental times was approximately equivalent to that of adult weights (high-quality diet: CV = 10.4 vs. 13.9; $Z = 1.3$, $P > 0.10$; low-quality diet: CV = 8.7 vs. 13.4; $Z = 1.9$, $P > 0.05$). On the high-quality diet, the CV of adult age in the Alaskan population was less than that in the Idaho population (5.4 vs. 10.4; $Z = 2.7$, $P < 0.01$), but this was not the case on the low-quality diet (6.5 vs 8.7; $Z = 1.3$, $P > 0.10$).

Alaskan grasshoppers consumed less food, in absolute terms, during the final two instars than did the Idaho grasshoppers, regardless of diet quality (Tables 3, 4). When adjusted for initial size of the fourth instars, Alaskan grasshoppers still consumed less than the Idaho grasshoppers on the high-quality diet but not on the low-quality diet (Tables 3, 4). When adjusted for the effects of size and time, population differences on the high-quality diet remained significant but much less so (Table 3). On the low-quality diet, there was a significant interaction effect between development time and population on food consumption ($F_{1,38} = 9.6$, $P = 0.004$), making it difficult to interpret the results. In the Alaskan population, individuals that required more time to reach adult molt tended to eat less food, suggesting nonacceptance of the diet, whereas the Idaho grasshoppers consumed the low-quality diet in proportion to developmental time (Fig. 2).

On the high-quality diet, there was a significant interaction between food consumption and population in their effect on assimilation ($F_{1,40} = 18.0$, $P < 0.001$). The slope of the regression was steeper for the Alaskan population than for the Idaho grasshoppers (Fig. 3). Comparisons of least squares means adjusted to levels of consumption between 250 and 330 mg were not significant ($P > 0.05$), but at consumption levels of 340 mg and greater, least squares means indicated greater rates of assimilation for the Alaskan grasshoppers ($P < 0.05$). Although the slopes of the regressions of food assimilated on food consumed differed statistically between the two populations, it is arguable that the difference between functions was not biologically significant. The intercept of the regression through the two populations combined was close to zero ($t = 0.5$, $P = 0.61$). The ratio of food assimilated to food consumed was nearly identical for the two populations (0.517 vs. 0.516 for Alaska and Idaho grasshoppers, respectively). Based on these considerations, I conclude that there was little or no difference in assimilation rates between the populations on the high-quality diet. On the low-quality diet, visual inspection of the plots of food consumed and food assimilated suggests differing relationships between populations (Fig. 4), but the interaction effect of population by consumption was not strong ($F_{1,38} = 3.3$, $P = 0.092$). Least squares means from ANCOVA (Table 4) showed greater rates of assimilation by the Alaskan grasshoppers than by the those from Idaho on the low-quality diet.

Analysis of efficiency of conversion of assimilated food to biomass was unencumbered by interactions with population. For the high-quality diet, results of ANCOVA showed that Alaskan grasshoppers gained more weight when corrected for assimilated food than the Idaho grasshoppers (Tables 3, 4), but on the low-quality diet, Alaskan grasshoppers gained less weight per assimilated food to weight gain than did the Idaho grasshoppers (Tables 3, 4).

On the high-quality diet, the N percentage in the cadavers was greater in the Alaskan grasshoppers than in the Idaho group (11.5% vs. 10.7% dry weight; $F_{1,20} = 13.1$, $P < 0.01$). Furthermore, on the high-quality diet there was lower N percentage in the feces of the Alaskan grasshoppers than in feces of Idaho grasshoppers (3.6% vs. 4.3% dry weight; $F_{1,42} = 152.9$, $P < 0.001$). On the low-quality diet, there were no differences between the populations in terms of N percentage of cadavers (11.0% vs. 11.0% dry weight; $F_{1,20} = 0.1$, $P > 0.10$) or feces (1.0% vs. 1.1% dry weight; $F_{1,40} = 0.3$, $P > 0.10$).

On the high-quality diet, the interaction of population by consumption had a significant effect on amount of nitrogen assimilated ($F_{1,40} = 9.7$, $P < 0.01$), but unlike the regressions for total food assimilated, the different population regressions of assimilated N on consumption did not cross at any point where the populations overlapped in terms of consumption (Fig. 5). Therefore, the Alaskan grasshoppers tended to assimilate more N from their food, or to retain N more efficiently, than the Idaho grasshoppers (Table 4). On the low-quality diet, the Alaskan grasshoppers assimilated more N, when corrected for consumption, than did the grasshoppers from Idaho (Tables 3, 4). For both diets, there was no difference between populations in the amount of weight gained in relation to the amount of N assimilated (Tables 3, 4).

Sex Effects

At the beginning of the fourth instar, males and females did not differ in size or age ($F < 2.0$, $P > 0.10$). On both diets, females gained more weight than males, although the difference was not as great on the low-quality diet (91.3 ± 3.0 vs. 77.1 ± 2.5 mg dry weight on the high-quality diet and 73.6 ± 2.5 vs. 65.7 ± 2.5 on the low-quality diet). Interactions

Table 3: *F* ratios from ANOVA and ANCOVA of food consumption, assimilation, and weight gain for *Melanoplus sanguinipes* reared on meridic diets through fourth and fifth instars

		Dependent Variable									
	df	Consumption			Assimilation		Net N Retained		Weight Gain		
High-quality diet:											
Covariables:											
Dry weight of fourth instar	1	…	.8	.8	…	…	…	…	…	…	…
Duration of fourth and fifth instars	1	…	…	2.3	…	…	…	…	…	…	…
Consumption (population)	2	…	…	…	…	108.2***	…	74.7***	…	…	…
Assimilation	1	…	…	…	…	…	…	…	…	45.1***	…
Net N retained	1	…	…	…	…	…	…	…	…	…	38.9***
Effects:											
Population	1	81.6***	47.1***	5.4*	50.2***	15.3**	14.6**	5.2*	7.3*	5.3*	.7
Sex	1	16.0**	16.2***	4.4*	5.0*	5.2*	4.2*	1.9	18.9***	10.4**	9.4**
Population × sex	1	2.4	2.1	.5	2.0	4.8*	1.9	1.8	.1	4.0	2.5
Low-quality diet:											
Covariables:											
Dry weight of fourth instar	1	…	11.8**	11.2**	…	…	…	…	…	…	…
Duration of fourth and fifth instars (population)	2	…	…	5.4*	…	…	…	…	…	…	…
Consumption	1	…	…	…	…	12.2**	…	161.3***	…	…	…
Assimilation	1	…	…	…	…	…	…	…	…	32.6***	…
Net N retained	1	…	…	…	…	…	…	…	…	…	6.7*
Effects:											
Population	1	8.4**	.2	7.4*	3.2	10.9**	.7	18.5**	.1	4.1*	.1
Sex	1	13.5**	10.6**	9.5**	11.3**	2.3	9.2**	.0	5.0*	.1	.8
Population × sex	1	.1	.2	.0	1.0	.9	.7	2.7	1.5	.5	.7

Note: Error df = 40 for high-quality diet and 38 for low-quality diet. Covariable followed by a main effect in parentheses was nested within that variable because of a significant interaction effect between the covariable and main effect. An ellipsis indicates that the given covariable was not included in the analysis.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Table 4: Least squares means (SE) by diet and population origin for nutritional indices of *Melanoplus sanguinipes* reared on meridic diets through fourth and fifth instars

	High-Quality Diet			Low-Quality Diet		
	Alaska		Idaho	Alaska		Idaho
Consumption	280.7 (8.5)	***	392.0 (11.3)	667.5 (24.5)	***	779.4 (32.1)
Consumption (dwt4)	286.1 (9.9)	***	388.4 (9.4)	720.8 (28.6)	n.s.	739.2 (24.9)
Consumption (dwt4, d[a])	305.0 (15.8)	*	370.8 (14.8)	698.1 (41.4)	n.a.	685.3 (28.8)
Assimilation	146.6 (6.4)	***	202.3 (8.9)	228.3 (8.9)	n.s.	212.3 (6.5)
Assimilation (consumption)	190.8 (4.3)	n.a.	179.6 (3.5)	237.0 (6.7)	**	205.9 (6.0)
Net N retained	8.7 (.3)	**	10.4 (.3)	6.5 (.3)	n.s.	6.9 (.3)
Net N retained (consumption)	11.0 (.3)	**	9.4 (.2)	7.3 (.2)	**	6.3 (.1)
Weight gain	59.0 (2.9)	*	68.3 (2.4)	48.6 (2.8)	n.s.	49.9 (1.8)
Weight gain (assimilation)	68.1 (2.0)	*	60.5 (1.9)	46.7 (1.7)	*	51.5 (1.5)
Weight gain (N retained)	66.8 (2.1)	n.s.	64.2 (1.7)	49.0 (2.2)	n.s.	49.7 (1.9)

Note: Data are presented with SE in parentheses. Means of variables followed by covariables in parentheses were adjusted for the effect of the covariable with ANCOVA. All values are in mg. dwt4 = dry weight at beginning of fourth instar. n.a. = comparisons between populations not applicable; n.s. = no significant difference between populations.

[a] Duration of fourth plus fifth instars.

* Populations different at $P < 0.05$.

** Populations different at $P < 0.01$.

*** Populations different at $P < 0.001$.

of population source with sex were weak or nonexistent ($F < 3.0$, $P > 0.05$), except for developmental time on the high-quality diet ($F_{1,42} = 8.7$, $P < 0.01$), where there was only a small difference between the sexes in the Alaskan grasshoppers (16.3 ± 0.37 vs.15.3 ± 0.31 d for females and males, respectively; $F_{1,19} = 4.1$, $P = 0.056$), but in the Idaho population, development time for females averaged about 3 d longer than that for males (22.0 ± 0.41 vs. 18.9 ± 0.34 d; $F_{1,21} = 34.0$, $P < 0.001$). On the low-quality diet, there was no difference between the sexes in terms of developmental times ($F_{1,40} = 0.3$, $P = 0.56$). Growth rate did not differ significantly between the sexes on either diet ($F < 0.5$, $P > 0.10$).

The ANCOVA for effects of sex was relatively straightforward because there was no collinearity or interactions of covariates and sex. Females consumed more food than males, even when values were adjusted for time and size (Table 3; least squares mean ± SE: 354.5 ± 9.9 vs. 321.2 ± 10.0 mg dry weight on the high-quality diet and 739.3 ± 28.5 vs. 644.1 ± 26.0 mg dry weight on the low-quality diet). Females assimilated more food than males on both diets, but only because they consumed more food. When adjusted for consumption, assimilation rates of females were lower on the high-quality diet (170.6 ± 2.9 vs. 180.6 ± 2.9 mg), and on the low-quality diet there was no difference between the sexes (Table 3). When corrected for consumption, N assimilation did not differ between sexes (Table 3). On the high-quality diet, females gained more weight when values were corrected for assimilated food (Table 3; 68.7 ± 1.7 vs. 59.8 ± 1.6 mg dry weight), and for assimilated N (69.6 ± 1.8 vs. 61.4 ± 1.9 mg dry weight). On the low-quality diet, there was no difference between the sexes in terms of efficiency of conversion of assimilated food or N use efficiency (Table 3).

Discussion

There are multiple forces that may exert selection on growth and developmental rates (Abrams et al. 1996; Chippindale et al. 1996; Fielding 2004*b*; Stoks et al. 2005), and season length, as measured by average frost-free days, may not always be a reliable indicator of selection pressure. For instance, daily max-

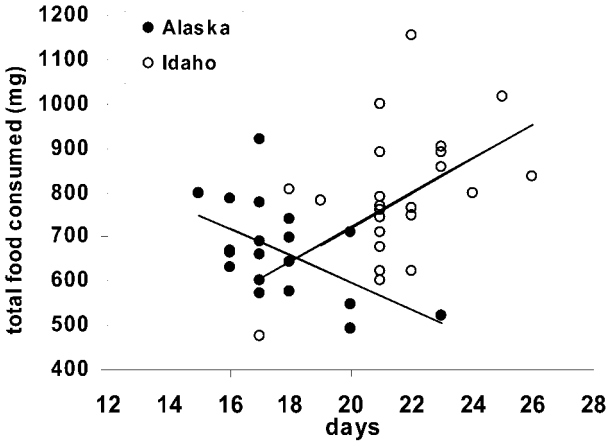

Figure 2. Relationship of total food consumed (low-quality diet) to number of days as fourth and fifth instars. *Open circles* = Idaho grasshoppers ($y = 38.9x - 56.0$, $r^2 = 0.24$); *filled circles* = Alaska grasshoppers ($y = -30.4x + 1{,}204$, $r^2 = 0.30$).

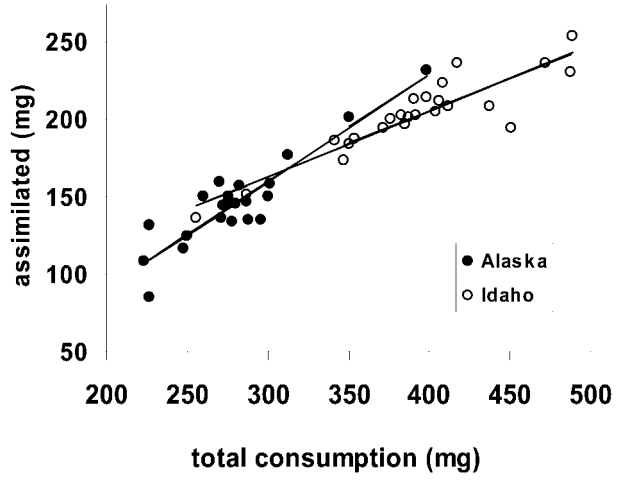

Figure 3. Relationship of total food assimilated to food consumed (high-quality diet) during fourth and fifth instars. *Open circles* = Idaho grasshoppers ($y = 0.426x + 35.6$, $r^2 = 0.82$); *filled circles* = Alaska grasshoppers ($y = 0.693x - 47.8$, $r^2 = 0.83$).

imum air temperatures in the summer in subarctic regions are marginal for grasshopper development, but, largely through behavioral thermoregulation (Chappell and Whitman 1990), the Alaskan population in nature completes development from egg hatch to adult molt in about the same amount of time as has been reported for grasshoppers from lower latitudes, from 40 to 50 d (Gage et al. 1976; Kemp and Onsager 1986; Fielding 2004*a*). It is also possible that poor food quality in late summer may select for rapid development so that grasshoppers can take advantage of the more favorable conditions of early summer. Nevertheless, the Alaskan grasshoppers developed more rapidly than the Idaho grasshoppers under all experimental conditions in this study. The low variability of developmental times is also consistent with strong, stabilizing selection on this trait in the Alaskan population. Developmental times tended to be more variable in the Idaho population.

The Alaskan grasshoppers achieved rapid development by means of greater growth rates and smaller final size. Although calculated growth rates are not directly comparable between the two experiments (because growth rate on the lettuce/bran diet was calculated from egg hatch to adult, using fresh weight, whereas growth rate on the meridic diet was calculated over only the final two instars, using dry weight), results were consistent in that Alaskan grasshoppers exhibited greater rates of growth in both sets of experiments. Ayres and Scriber (1994) found that more rapid growth in *Papilo canadensis* caterpillars from Alaska was enabled primarily by greater rates of consumption, at least at lower temperatures. Kause et al. (1999) described positive phenotypic correlations between growth rate and consumption and efficiency of conversion of ingested food. In this study, more rapid growth of the Alaskan grasshoppers was supported by increased postingestive efficiencies but not by increased consumption. On the high-quality diet, rapid growth by the Alaskan grasshoppers was accompanied by a greater allocation of assimilated food to growth, whereas on the low-quality diet, rapid growth of the Alaskan grasshoppers was associated primarily with greater rates of assimilation. On both diets, the Alaskan grasshoppers had the advantage of greater net retention of N. This suggests that the Alaskan grasshoppers may have a higher protein requirement than Idaho grasshoppers. The concentration of N in the carcasses was greater for the Alaskan grasshoppers on the high-quality diet. The greater concentration of N could be due to lower lipid content in the Alaskan grasshoppers, but it would seem that if this were the case, the Idaho grasshoppers would show greater weight gain per unit of N assimilated, which was not the case. Efficiencies in N metabolism could be due to higher levels of assimilation (higher levels of proteolytic enzymes) or more efficient retention or recycling of N, through production of thinner peritrophic membranes, for example. Studies are planned that will further investigate the N demand and lipid content of the two populations.

Predation has been implicated as a cost of rapid growth (Gotthard 2000; Danner and Joern 2003; McPeek 2004; Stoks et al. 2005), perhaps because rapidly growing animals require more food and spend more time actively foraging and thus are more exposed to predators. In this study, the Alaskan grasshoppers consumed smaller or similar amounts of food compared to the slower-growing Idaho grasshoppers, and so they may not be expected to be at greater risk of predation. But the relationships among activity, feeding, and predation may not always be straightforward. McPeek (2004), comparing growth, activity, feeding, and predation between two species of damselfly, found that the more active, and faster growing, species suffered greater predation but also that the increased activity

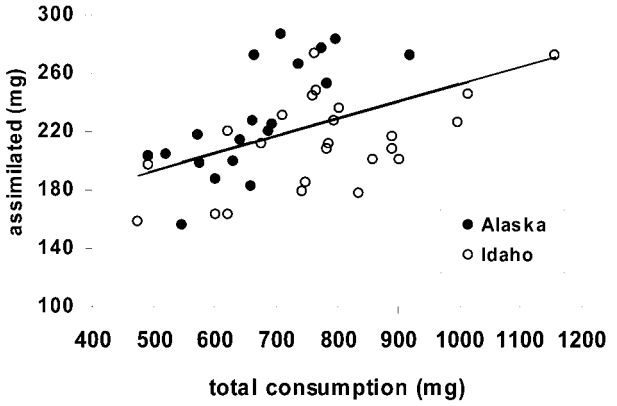

Figure 4. Relationship of total food assimilated to food consumed during fourth and fifth instars (low-quality diet; $y = 0.107x + 141.6$, $r^2 = 0.20$). *Open circles* = Idaho grasshoppers; *filled circles* = Alaska grasshoppers.

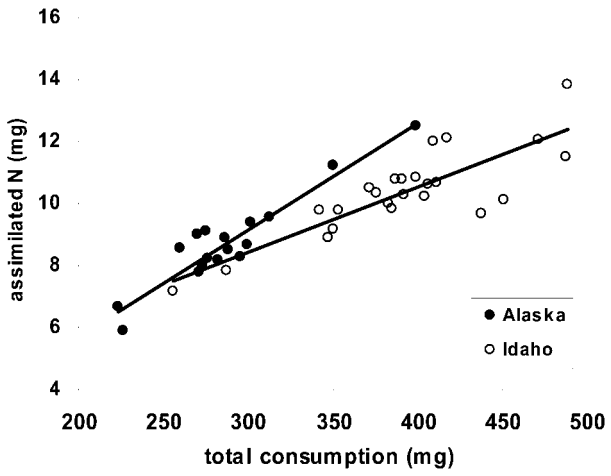

Figure 5. Relationship of net N retention to total food consumed (high-quality diet). *Open circles* = Idaho grasshoppers ($y = 0.021x + 2.07$, $r^2 = 0.70$); *filled circles* = Alaska grasshoppers ($y = 0.035x - 1.24$, $r^2 = 0.89$).

was not associated with increased feeding. As for the grasshoppers in this study, faster growth rates in the damselflies were associated with enhanced postingestive efficiencies.

Controlled temperatures were used in this study, rather than allowing the grasshoppers to self-select their preferred temperatures. The objective of this study was to compare growth and developmental rates between the two populations, which required that the grasshoppers experience the same temperatures. The experimental conditions were selected to provide comparisons over a range of temperatures. Although grasshoppers typically self-select body temperatures higher than those used in this study (Chappell and Whitman 1990), previous experiments have shown that survival and adult weight are maximal when grasshoppers are reared at constant temperatures of 30°–33°C (Fielding 2004*a*). The large difference in developmental times between populations at 22°C on the lettuce/bran diet was probably exaggerated by the high mortality of the Alaskan grasshoppers at this temperature. If less vigorous, slower-growing individuals did not survive, results would be biased toward the more rapidly developing portion of the population. It may be expected that the Alaskan population would be better adapted to these low temperatures, but it is possible that the Alaskan population has evolved thermal performance curves that maximize developmental rates at high temperatures (Gilchrist 1995). Comparison of developmental rates of the Alaskan population with those of published data for this species from more temperate climates (Fielding 2004*a*) indicates that the Alaska population has a temperature optimum similar to those of other populations and also is not a temperature generalist (Gilchrist 1995). Even though the Alaskan population may experience relatively cool temperatures more frequently than the Idaho population, they apparently do not have a lower temperature optimum, at least in terms of developmental rates. It may be that to optimize growth and development at cooler temperatures would result in a decline in their maximum intrinsic rate of increase, r_{max}. Frazier et al. (2006), in an analysis of published reports of r_{max} in insects, present evidence that r_{max} is greater in populations with higher optimal temperatures; that is, species are not able to compensate completely, in terms of r, for adaptation to cooler temperatures. Through thermoregulation, Alaskan grasshoppers may be able to maintain high body temperatures frequently enough that adaptation to cooler temperature would not be worth the cost of lower r.

Grasshoppers are well known to increase consumption to compensate for low levels of nutrients (Yang and Joern 1994; Berner et al. 2005). Concentration of nutrients in the low-quality diet was about one-third that in the high-quality diet, but consumption of the two diets differed by only a factor of about 2. Less weight gain and slower growth on the low-quality diet by both populations indicates that the concentration of nutrients was below the level at which the grasshoppers could compensate by increasing consumption. The fact that time and size had strong effects on food consumption on the low-quality diet but not the high-quality diet (Table 3) also suggests that the grasshoppers were at the limit of their capacity to consume and process enough food to compensate for the low concentration of nutrients. If grasshoppers were feeding at capacity, then allowing more time to feed would increase overall consumption. But if grasshoppers were getting enough nutrients without feeding to capacity, then consumption might not be as likely to increase with more time or larger size.

We had hypothesized that the Alaskan grasshoppers would be more sensitive to low-quality diets than the Idaho grasshoppers, but there is little to suggest that the Alaskan grasshoppers fared any worse on the low-quality diet than did the Idaho grasshoppers. The Alaskan grasshoppers grew and developed faster than the Idaho grasshoppers on both diets. Alaskan grasshoppers maintained greater net retention of N than the Idaho grasshoppers on both diets. Furthermore, on the low-quality diet, there was no difference in weight gain between the populations, whereas on the high-quality diet, the Idaho grasshoppers gained more weight than the Alaskan grasshoppers; that is, the grasshoppers from Idaho suffered a relatively greater reduction in weight gain on the low-quality diet than on the high-quality diet. The relative difference between populations in the total amount of food consumed was also less on the low-quality diet than on the high-quality diet. The Alaskan grasshoppers lost their advantage over the Idaho grasshoppers in the conversion of assimilated food to biomass on the low-quality diet but apparently increased their assimilation on the low-quality diet relative to the Idaho grasshoppers (Table 4). The Alaskan grasshoppers also maintained a higher assimilation rate of N than the Idaho grasshoppers on both diets. It may be that there are other costs besides sensitivity to diet quality associated with higher growth rates, such as lowered resistance

to starvation, pathogens, or other forms of stress, but these were not examined here. The poor survival of the Alaskan grasshoppers at cool constant temperatures (22°C) could be an indicator of lowered resistance to stress, but this will need to be explored in greater detail before any conclusions can be drawn.

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Literature Cited

Abrams P.A., O. Leimar, S. Nylin, and C. Wiklund. 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. Am Nat 147:381–395.

Arendt J.D. 1997. Adaptive growth rates: an integration across taxa. Q Rev Biol 72:149–177.

Ayres M.P. and J.M. Scriber. 1994. Local adaptation to regional climates in *Papilio canadensis* (Lepidoptera: Papilionidae). Ecol Monogr 64:465–482.

Belovsky G.E. and J.B. Slade. 1995. Dynamics of two Montana grasshopper populations: relationships among weather, food abundance and intraspecific competition. Oecologia 101: 383–396.

Belovsky G.E., J.B. Slade, and B.A. Stockhoff. 1990. Susceptibility to predation for different grasshoppers: an experimental study. Ecology 71:624–634.

Bentz B.J., J.A. Logan, and J.C. Vandygriff. 2001. Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. Can Entomol 133: 375–387.

Berner D., W.U. Blanckenhorn, and C. Korner. 2005. Grasshoppers cope with low host plant quality by compensatory feeding and food selection: N limitation challenged. Oikos 111:525–533.

Berner D., C. Korner, and W.U. Blanckenhorn. 2004. Grasshopper populations across 2000 m of altitude: is there life history adaptation? Ecography 27:733–740.

Branson D.H. 2004. Relative importance of nymphal and adult resource availability on reproductive allocation in *Melanoplus sanguinipes* (Orthoptera: Acrididae). J Orthoptera Res 13: 239–245.

———. 2005. Direct and indirect effects of avian predation on grasshopper communities in northern mixed-grass prairie. Environ Entomol 34:1114–1121.

Capinera J.L., C.W. Scherer, and J.M. Squitier. 2002. Grasshoppers of Florida. University Press of Florida, Gainesville.

Chappell M.A. and D.W. Whitman. 1990. Grasshopper thermoregulation. Pp. 143–172 in R.F. Chapman and A. Joern, eds. Biology of Grasshoppers. Wiley, New York.

Chippindale A.K., T.J.F. Chu, and M.R. Rose. 1996. Complex trade-offs and the evolution of starvation resistance in *Drosophila melanogaster*. Evolution 50:753–766.

Danner B.J. and A. Joern. 2003. Resource-mediated impact of spider predation risk on performance in the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). Oecologia 137: 352–359.

Dingle H., T.A. Mousseau, and S.M. Scott. 1990. Altitudinal variation in life cycle syndromes of California populations of the grasshopper, *Melanoplus sanguinipes* (F.). Oecologia 84:199–206.

Elliot S.L., S. Blanford, and M.B. Thomas. 2002. Host-pathogen interactions in a varying environment: temperature, behavioural fever and fitness. Proc R Soc Lond B 269:1599–1607.

Fielding D.J. 2004*a*. Developmental time of *Melanoplus sanguinipes* F. (Orthoptera: Acrididae) at high latitudes. Environ Entomol 33:1513–1522.

———. 2004*b*. Intraspecific competition and spatial heterogeneity alter life history traits in an individual based model of grasshoppers. Ecol Model 175:169–187.

———. 2006. Optimal diapause strategies of a grasshopper, *Melanoplus sanguinipes*. J Insect Sci 6, article 2. http://insectscience.org/6.02.

Fischer K. and K. Fiedler. 2002. Reaction norms for age and size at maturity in response to temperature: a test of the compound interest hypothesis. Evol Ecol 16:333–349.

Frazier M.R., R.B. Huey, and D. Berrigan. 2006. Thermodynamics constrains the evolution of insect population growth rates: "warmer is better." Am Nat 168:512–520.

Gage S.H., M.K. Mukerji, and R.L. Randell. 1976. A predictive model for seasonal occurrence of three grasshopper species in Saskatchewan (Orthoptera: Acrididae). Can Entomol 108: 245–253.

Gilchrist G.W. 1995. Specialists and generalists in changing environments. 1. Fitness landscapes of thermal sensitivity. Am Nat 146:252–270.

Gotthard K. 2000. Increased risk of predation as a cost of high growth rate: an experimental test in a butterfly. J Anim Ecol 69:896–902.

———. 2004. Growth strategies and optimal body size in temperate Pararginii butterflies. Integr Comp Biol 44:471–479.

Gotthard K., S. Nylin, and C. Wiklund. 1994. Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, *Parage aegeria*. Oecologia 99:281–289.

Henry J.E. 1985. *Melanoplus* spp. Pp. 451–464 in P. Singh and R.F. Moore, eds. Handbook of Insect Rearing. Vol. 1. Elsevier, New York.

Inglis G.D., D.L. Johnson, and M.S. Goettel. 1996. Effects of temperature and thermoregulation on mycosis by *Beauveria bassiana* in grasshoppers. Biol Control 7:131–139.

Kause A., I. Saloniemi, E. Haukioja, and S. Hanhimaki. 1999. How to become large quickly: quantitative genetics of growth and foraging in a flush feeding lepidopteran larva. J Evol Biol 12:471–482.

Kemp W.P. and J.A. Onsager. 1986. Rangeland grasshoppers (Orthoptera: Acrididae): modeling phenology of natural populations of six species. Environ Entomol 15:924–930.

Margraf N., K. Gotthard, and M. Rahier. 2003. The growth strategy of an alpine beetle: maximization or individual growth adjustment in relation to seasonal time horizons? Funct Ecol 17:605–610.

McPeek M.A. 2004. The growth/predation risk trade-off: so what is the mechanism? Am Nat 163:E88-E111.

Miller G.E. 1991. Asymptotic test statistics for coefficients of variation. Commun Stat Theor Math 20:2251–2262.

Nylin S. and K. Gotthard. 1998. Plasticity in life-history traits. Annu Rev Entomol 43:63–83.

Packard G.C. and T.J. Boardman. 1988. The misuse of ratios, indices, and percentages in ecophysiological research. Physiol Zool 61:1–9.

Parker J.R. 1930. Some Effects of Temperature and Moisture upon *Melanoplus mexicanus mexicanus* Saussure and *Camnula pellucida* Scudder (Orthoptera). Mont Agric Exp Stn Bull 223.

Pfadt R.E. 2002. Field Guide to Western Grasshoppers. 3rd ed. Wyo Agric Exp Stn Bull 912.

Raubenheimer D. 1995. Problems with ratio analysis in nutritional studies. Funct Ecol 9:21–29.

Raubenheimer D. and S.J. Simpson. 1992. Analysis of covariance: an alternative to nutritional indices. Entomol Exp Appl 62:221–231.

Richman D.B., D.C. Lightfoot, C.A. Sutherland, and D.J. Ferguson. 1993. A Manual of the Grasshoppers of New Mexico. Orthoptera: Acrididae and Romalidae. New Mexico State University Cooperative Extension Service, Las Cruces.

Roff D.A. 1992. The Evolution of Life Histories: Theory and Analysis. Chapman & Hall, New York.

Salt R.W. 1949. A key to the embryological development of *Melanoplus bivittatus* (Say), *M. mexicanus mexicanus* (Sauss.), and *M. packardii* Scudder. Can J Res 27:179–191.

SAS Institute. 2001. SAS for Windows. Release 8.02. SAS Institute, Cary, NC.

Schmidt D.J. and J.C. Reese. 1986. Sources of error in nutritional index studies of insects on artificial diet. J Insect Physiol 32:193–198.

Simpson S.J. and D. Raubenheimer. 1993. A multi-level analysis of feeding behaviour: the geometry of nutritional decisions. Philos Trans R Soc B 342:381–402.

Stockhoff B.A. 1991. Starvation resistance of gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae): tradeoffs among growth, body size, and survival. Oecologia 88:422–429.

Stoks R., M. De Block, F. Van de Meutter, and F. Johansson. 2005. Predation cost of rapid growth: behavioural coupling and physiological decoupling. J Anim Ecol 74:708–715.

Tammaru T., S. Nylin, K. Ruohomaki, and K. Gotthard. 2004. Compensatory responses in lepidopteran larvae: a test of growth rate maximisation. Oikos 107:352–362.

Telser M.G. and M. Hassall. 1999. Ecotypic differentiation in the grasshopper *Chorthippus brunneus*: life history varies in relation to climate. Oecologia 121:245–254.

Watler D. 1982. Influence of social situation on food consumption and growth in nymphs of the house cricket, *Acheta domesticus*. Physiol Entomol 7:343–350.

WRCC. 2004. Western Regional Climate Center. Desert Research Institute, Reno, NV. http://www.wrcc.dri.edu/index.html.

Yang Y. and A. Joern. 1994. Compensatory feeding in response to variable food quality by *Melanoplus differentalis*. Physiol Entomol 19:75–82.

Zar J.H. 1999. Biostatistical Analysis. 4th ed. Prentice Hall, Upper Saddle River, NJ.